

Gerbillidae from the Miocene and Pliocene of Europe

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With 4 figures, 3 plates, 2 tables and 2 appendixes

Abstract

In this paper the distribution of Miocene and Pliocene Gerbillidae in Europe is described. It appears that only a few species of this family were present for only a short period of time (Upper Miocene-Lower Pliocene). The European Gerbillidae are related to forms from North Africa and Asia Minor and are thought to have immigrated in, at least, two waves during the Upper Miocene and Lower Pliocene into Europe.

Kurzfassung

In dieser Arbeit wird die Verbreitung von miozänen und pliozänen Gerbillidae in Europa besprochen. Nur wenige Arten dieser Familie traten für einen kurze Zeitraum auf. Die europäischen Gerbillidae sind mit nordafrikanischen und kleinasiatischen Arten verwandt. Es wird angenommen, daß sie in mindestens zwei Wellen während des Obermiozäns und Unterpliozäns nach Europa eingewandert sind.

Introduction

Only a few Gerbillidae species from the Miocene of Europe are recorded in the literature until now. The family seems to be of minor importance in the Miocene fauna's of Europe and moreover most of these genera and species were present for only a short time (appendix 1). However the species found in the European Miocene are part of a complex story of evolutionary history, with migrations, dispersions, extinctions and many uncertain origins.

First a general overview of the family is given, followed by a short introduction into the taxonomy, after which, in more detail, an overview of the three subfamilies is given with emphasis on fossil occurrences (only cheek teeth) especially those from Europe. Possible migration routes during and after the Messinian used by the European Gerbillidae are given at the end of this chapter.

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The Family Gerbillidae

The family Gerbillidae¹ (Table I) is represented by 16 extant genera and many species which occur mainly in (semi-)desert environments in Africa, the Arabian Peninsula and Asia. Extant Gerbillidae are not known from Europe. Some species are very well known because they are popular as pets (Internet: Gerbil Information Page) or used for laboratory research (*Meriones unguiculatus*) or are considered to be a plague, damaging and destroying crops and undermining irrigation works by their intensive burrowing and spreading diseases (*Tatera*, *Rhombomys*) (PRAKASH, 1975; NOWAK, 1991). Gerbillidae make simple or complex burrow systems for protecting their offspring or creating shelters against the dry and hot climate. Most of them are granivorous and some also insectivorous (PRAKASH, 1975; MUSSEY & CARLETON, 1991; NOWAK, 1991). Gerbillidae are modified for terrestrial plains or desert life, they have a tendency for the hind limbs to be lengthened and the tail is normally fully haired. The cheek teeth are extremely hypsodont in progressive species, with continuously growing teeth in very specialised forms (*Rhombomys*). The cusps form transverse laminae which are separated by inner and outer folds (sinuses and sinusids). In primitive forms the teeth are not always separated into laminae (and are cuspidate), the sinuses are weaker and each lamina bears clear traces of two cusps (except the anterocone which has only one cusp). The M³ is reduced (absent in *Desmodilliscus*), often cylindrical. The posterior lamina on M₃ is usually absent. The incisors may have a single groove, a faint double groove or be smooth. The outer enamel layers of the incisors are relative thin compared to other muroids (ELLERMAN, 1941; MUSSEY & CARLETON, 1991).

The family is divided into the subfamilies Myocricetodontinae, Taterillinae and Gerbillinae.

Taxonomy

Several papers concerning research on extant and fossil members of the Gerbillidae are listed in MUSSEY & CARLETON (1991), many authors studied cytogenetic-, chromosomal-, biochemical-, anatomical-, physiological-, and fossil data.; a few examples are LAY (1972), TONG (1989) and BENAZZOU et al. (1984). These studies resulted in several taxonomical classifications of the Gerbillidae, between which large differences exist in the number of extant species (88-110), subspecies, subgenera or subfamilies (ELLERMAN, 1941; CHALINE et al., 1977; TONG, 1989; PAVLINOV et al., 1990; MUSSEY & CARLETON, 1991; NOWAK, 1991). TONG (1989, page 110) concluded after combining the results of several research methods that a comprehensive taxonomical division of the Gerbillidae is impossible, but that the results illustrate the diverse patterns in the evolution of several characters.

In this paper we mainly deal with fossil material which largely consists of cheek teeth. The classification used in Table I² is therefore a classification in which morphology of the skull and cheek teeth are main elements. The classification of extant Gerbillinae from ELLERMAN (1941), who gives clear and consistent descriptions of extant genera and species, is extended with information on fossil Gerbillinae from a.o. CHALINE et al. (1977), TONG (1989) and WESSELS (1996).

¹ The ancestral group of this family lies probably in the Myocricetodontinae, therefore the family name should be Myocricetodontidae (WESSELS, 1996). But according to the International Code of Zoological Nomenclature the family name has to be Gerbillidae in agreement to the principle of priority.

² *Epimeriones* DAXNER-HÖCK (1972) (from the Miocene and/or Pliocene of Central Europe and Spain) is not included in the Gerbillidae (see DE WEERD et al., 1977; TONG, 1989).

Table I: The family Gerbillidae

Subfamily **Myocricetodontinae** LAVOCAT 1961

- Mystromys*³ WAGNER 1841
- Calomyscus*³ THOMAS 1905
- Myocricetodon*² LAVOCAT 1952
- Zramys*² JAEGER, MICHAUX & DAVID 1973
- Dakkamys*² JAEGER 1977a
- Mellalomys*² JAEGER 1977a
- Shamalina*² WHYBROW et al. 1982
- Punjabemys*² LINDSAY 1988
- Aïssamys*² COIFFAIT 1991
- Sindemys*² WESSELS 1996

Subfamily **Taterillinae** CHALINE, MEIN & PETTER 1977

- Tatera*³ LATASTE 1882
- Taterillus*³ THOMAS 1910b
- Gerbillurus*³ SHORTRIDGE 1942
- Protatera*² JAEGER 1977b
- Abudhabia*² DE BRUIJN & WHYBROW 1994

Subfamily **Gerbillinae** ALSTON 1876

- Gerbillus*³ DESMAREST 1804
- Meriones*³ ILLIGER 1811
- Psammomys*³ CRETZCHMAR 1828
- Pseudomeriones*² SCHAUB 1934
- Rhombomys*³ WAGNER 1841
- Pachyuromys*¹ LATASTE 1880
- Ammodillus*¹ THOMAS 1904
- Desmodillus*¹ THOMAS & SCHIWANN 1904
- Microdillus*¹ THOMAS 1910a
- Desmodilliscus*¹ WETTSTEIN 1917
- Brachiones*¹ THOMAS 1925
- Sekeetamys*¹ ELLERMAN 1947
- Mascaromys*² TONG 1986
- Eulmus*² AMEUR 1991
- Debruijnimys*² CASTILLO & AGUSTI 1996

¹ only extant

² only fossil

³ extant and fossil

The most important characteristics for differentiating the genera in ELLERMAN (1941) are based on cranial- and cheek teeth characters as well as length and shape of the tail. For the skull and mandible these are: mandible with or without a coronoid process; size of mastoids and bullae; size and shape of the palatal foramina; size and shape of the zygomatic plate and shape of the skull (size of the frontals, size and shape of the rostrum). For the cheek teeth these are: ever growing or with roots; upper incisors: plain or grooved; hypsodont or bunodont; laminae with or without the original cusps; prismatic laminae; absence/presence of a third lower molar and absence/presence of a longitudinal crest.

A schematic overview of the characteristics of the extant and fossil Gerbillidae genera can be found in TONG (1989). Since then more fossil genera have been described. Table II gives

characteristics of the genera known from Miocene and/or Pliocene localities. Only cheek teeth characters are used, since these are usually the only fossil material available.

Characterisation of cheek teeth-elements on subfamily level

Myocricetodontinae	Taterillinae	Gerbillinae
presence of a 'normal' or 'new' longitudinal crest in most	strong reduction or absence of a longitudinal crest	development of a 'new' longitudinal crest
alternating cusps	cusps in rows (laminae)	alternating cusps and/or cusps in rows (laminae)
cingula usually present	reduction of the cingula	reduction of the cingula
M ₃ still has 2 'lobes'	strong reduction of M ³ and M ₃	strong reduction of M ³ and M ₃
accessory cusp(s) on lingual edge M ¹		

Subfamily Myocricetodontinae

Myocricetodontinae are mainly known from the fossil record, its only extant members are *Calomyscus bailwardi* and *Mystromys albicaudatus*. The oldest Myocricetodontinae described until now is *Sindemys*³ from the upper Lower Miocene of Pakistan (WESSELS, 1996). A primitive species still with a „normal“ longitudinal crest and a mesoloph(id). A more primitive, but yet

Table II: Characteristics of Miocene and Pliocene Gerbillidae genera

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27		
Myocricetodontinae	<i>Sindemys</i>	■										■	■	■	■					■								-		
	<i>Punjabemys</i>		■									■	■	■	■					■									-	
	<i>Shamalina</i>	■										■	■	■	■					■		■		■					-	
	<i>Dakkamys</i>	■										■	■	■	■									■						
	<i>Mellalamys</i>	■	■									■	■	■	■						■		■	■						
	<i>Zramys</i>	■	■									■	■	■	■						■		■							
	<i>Myocricetodon</i> (A)			■	■								■	■								■		■	■					
	<i>Myocricetodon</i> (B)							■				■	■	■	■							■		■	■					
	<i>Calomyscus</i>	■											■	■	■	■					■				■					
	<i>Mystromys</i>	■											■	■	■	■										■				
	<i>Aïssamys</i>		■										■	■	■	■														-
Taterillinae	<i>Protatera</i>			■	■			■			■				■				■		■		■				■	■		
	<i>Tatera</i>			■	■									■	■	■			■		■		■		■		■	■		
	<i>Abudhabia</i>			■	■									■	■	■				■		■	■				■	■		
	<i>Taterillus</i>			■	■										■	■	■			■		■		■			■	■		
Gerbillinae	<i>Pseudomeriones</i>							■			■	■	■	■	■						■		■		■			■		
	<i>Mascaromys</i>						■			■		-	■			■	■	■	■	-		■		■	■	■	■	■		
	<i>Meriones</i>						■		■			■	■			■	■		■		■		■		■	■	■	■		
	<i>Eulmus</i>						■				■	■	■	■	■						■		■		■	■	■	-	-	
	<i>Debruijnimys</i>			■	■							■	■			■	■	■			■		■		■		-	-		
	<i>Gerbillus</i>			■	■	■			■			■	■			■	■	■			■		■				■	■		

■ in almost (all) specimens ■ in some specimens 1 only M₁
 ■ in many specimens □ none 2 only M₂
 ▴ in 50% - unknown 3 often weakly developed

³ *Primus* (Murree FM, Early Miocene of Pakistan, DE BRUIJN et al., 1981) is possibly a member of the Myocricetodontinae, but more material and research is needed on this genus to determine its family rank.

undescribed, myocricetodontine is known from Keşeköy (MN3, Turkey). In the Middle Miocene several Myocricetodontinae genera appeared (WESSELS, 1996). Some genera had a large geographical and stratigraphical distribution, for example *Myocricetodon* was present (Fig.1) for a long timespan in Pakistan (Sehwan and Potwar Plateau), North Africa (The Maghreb) and Namibia (Otavi Mountains) and for a short period of time in Turkey (Yeni Eskihisar), Kenya (Fort Ternan), Spain (Almenara-M) and France (La Tour). Not only *Myocricetodon* shows a wide geographical range of occurrences, *Mellalomys* and *Dakkamys* appear in Middle and Upper Miocene deposits of Pakistan, North Africa and probably Namibia (South Africa). Other Myocricetodontinae genera were successful (long time span) but did not migrate to other areas: *Zramys* is only known from the Middle and Late Miocene of North Africa (Appendix II). At the end of the Miocene almost all Myocricetodontinae vanished from the fossil record (except *Calomyscus*) and by then the first members of the Taterillinae had appeared in North Africa.

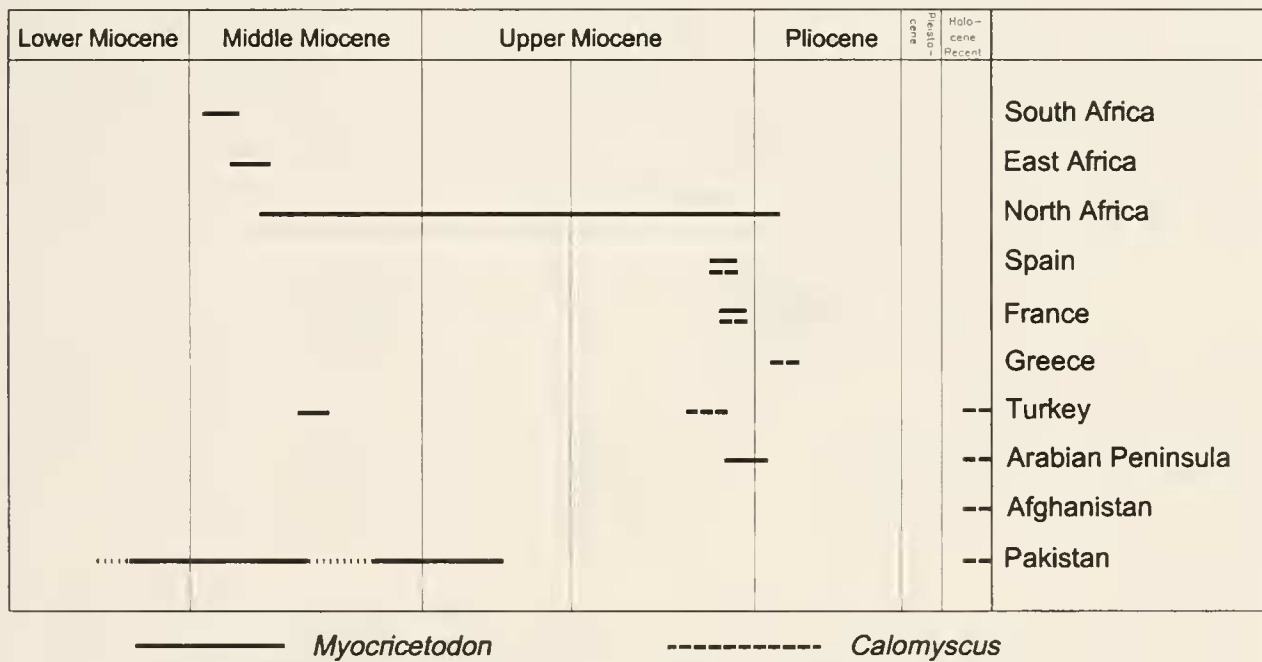


Figure 1: Distribution of Myocricetodontinae: *Myocricetodon* and *Calomyscus*

Longitudinal connections

1 - 'normal' longitudinal crest; 2 - 'normal' longitudinal crest but oblique; 3 - 'normal' longitudinal crest absent (upper molars); 4 - 'normal' longitudinal crest absent (lower molars); 5 - 'new' longitudinal crest, on labial or lingual edge (upper molars); 6 - 'new' longitudinal crest, in centre (upper molars); 7 - 'new' longitudinal crest, oblique (upper molars); 8 - 'new' longitudinal crest, on labial or lingual edge (lower molars); 9 - 'new' longitudinal crest, in centre (lower molars); 10 - 'new' longitudinal crest, oblique (lower molars)

11 - anterolophule (M^1) absent; 12 - anterolophulid (M_1) absent

Placement of the cusps

13 - alternating cusps (upper molars); 14 - alternating cusps (lower molars); 15 - transverse rows of cusps (upper molars); 16 - transverse rows of cusps (lower molars); 17 - strong laminae with cusps still clear; 18 - strong laminae, cusps incorporated

Divers characters

19 - mesoloph(id); 20 - simple anterocone; 21 - paraconus spur; 22 - (most) cingula reduced; 23 - accessory cusps; 24 - high crowned; 25 - M^3 one lobe; 26 - M_3 one lobe; 27 - upper incisors grooved

Myocricetodon is reported from four Upper Miocene South European localities: Salobreña (Plate 1, figs. 1, 2), Almenara-M and Pino Mojón in Spain and La Tour in Southern France. They resemble Moroccan *Myocricetodon* species from Afoud-5 and Lissasfa (GERAADS, 1998b) and probably migrated from Northern Africa into Spain during the Late Miocene.

Myocricetodon species can be divided into two groups (WESSELS, 1996). Group A includes all the species with a (almost) reduced 'normal' longitudinal crest, the tendency of arrangement of the cusps of the cheek teeth in transverse rows and the presence of the simple anterocone in M^1 . *Myocricetodon* species from group A occur in north, east and south Africa, their morphology could be seen as being ancestral to the Gerbillinae and/or Taterillinae (JAEGER 1977, TONG & JAEGER, 1993). Species of *Myocricetodon* group B show a large geographical distribution area: Pakistan, east, north and south Africa, Turkey, the Arabian Peninsula and Spain. The origin and migration pattern of *Myocricetodon* is not clear. Undescribed specimens from Keşeköy (MN3, coll. Utrecht) of primitive Myocricetodontinae and from some localities from Namibia (coll. Mein) may give more information in the future.

Calomyscus (Plate 1) is considered to be a member of the Myocricetodontinae (AGUSTÍ, 1989). *Calomyscus* sp. is known from the Upper Miocene from Turkey (Süleimanlı; DE BRUIJN pers. comm.), *Calomyscus* cf. *minor* and *Calomyscus delicatus* from the Upper Miocene of Spain (Salobreña; AGUILAR et al., 1984), *Calomyscus* sp. from the Upper Miocene of France (La Tour; JAEGER & HARTENBERGER, 1989) and *Calomyscus minor* from the Lower Pliocene of Greece (Maritsa; DE BRUIJN et al., 1970). *Calomyscus bailwardi* is the only extant species. The main difference between all the *Calomyscus* species is size. *Calomyscus delicatus* is the smallest,

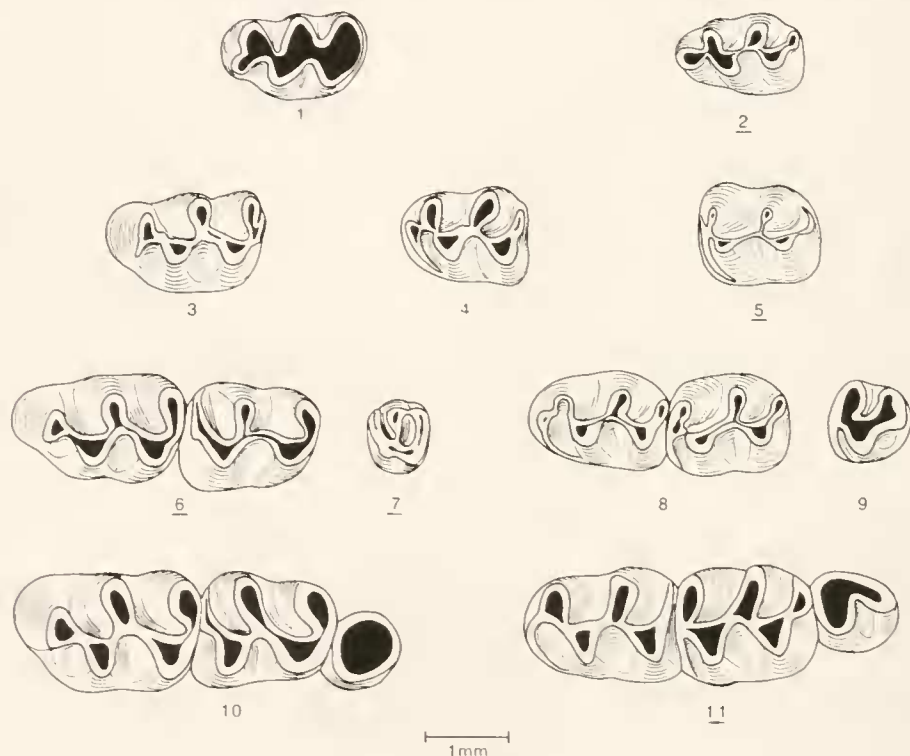


Plate 1: *Myocricetodon* sp. from Salobreña (Spain): fig. 1 M^1 sin (SAL114), fig. 2 M_1 dex (SAL115), AGUILAR et al., 1984.

Calomyscus delicatus from Salobreña (Spain): fig. 3 M^1 (SAL109, holotype), fig. 4 M_1 sin (SAL97), fig. 5 M_2 dex (SAL102), AGUILAR et al., 1984.

Calomyscus minor from Rhodos (Greece): fig. 6 M^{1-2} dex (no 786, holotype), fig. 7 M^3 dex (no 881), fig. 8 $M_{1,2}$ sin (no 640), fig. 9 M_3 sin (no 728), DE BRUIJN et al., 1970.

Calomyscus bailwardi (Recent): fig. 10 M^{1-3} sin (B.M.), fig. 11 $M_{1,3}$ dex (B.M.), DE BRUIJN et al. 1970.

All specimens are figured as left cheek teeth; an underlined number denotes that the original is from the right side.

C. bailwardi the largest. The origin of *Calomyscus*, a myocricetodontine with a simple anterocone (M¹) and a 'normal' longitudinal crest, is unknown. Some (undescribed) Myocricetodontinae from the Middle Miocene of Namibia (MEIN, pers. comm.) show these characters, but whether a relation exists with *Calomyscus* is unclear. The occurrences of *Calomyscus* in Europe and their absence in Africa during the Miocene and Pliocene indicate an (West)Asiatic origin with a dispersal at the end of the Miocene to Europe and Asia Minor. At the present day *Calomyscus bailwardi* is known from Syria, Turkmenistan, Azerbaidzhan, Iran, Afghanistan and Pakistan. It inhabits elevated areas of 400-3500 metres altitude, between evergreen oaks in monsoonal areas as well as barren scorched hills (NOWAK, 1991).

Subfamily Taterillinae

The origin of the Taterillinae lies probably in a species with a morphology of *Myocricetodon* group A (TONG, 1989; DE BRUIJN & WHYBROW, 1994; WESSELS 1996), these are characterised by the absence (in most specimens) of the longitudinal crest, the tendency to arrange cusps of the cheek teeth in transverse rows and by the presence of a simple anterocone (M¹).

Two genera appear in the upper Miocene (Fig. 2): *Protatera*, who is considered to be the ancestor of *Tatera* (JAEGER, 1977b) and *Abudhabia* (Plate 2), who is a possible ancestral form to *Taterillus* (DE BRUIJN & WHYBROW, 1994).

Protatera algeriensis (Plate 2, figs. 1-6), the oldest Taterillinae described until now is considered to be the ancestral form to *Protatera almenarensis* (Plate 2, figs. 7-12) from the Spanish Upper Miocene localities Almenara-M and Salobreña (AGUSTÍ, 1991). The oldest *Tatera* has been reported from the Lower Pliocene locality of Langebaanweg, South Africa (HENDEY, 1981). Later *Tatera* occurrences have been reported from several Pliocene and Pleistocene localities from East and South Africa (Appendix II). Extant *Tatera* species are common in many regions in Africa. Only one species, *Tatera indicus*, occurs outside of Africa, from Syria to India and Sri Lanka. *Tatera* inhabits grasslands, sandy plains and savannahs, but also woodlands and cultivated areas.

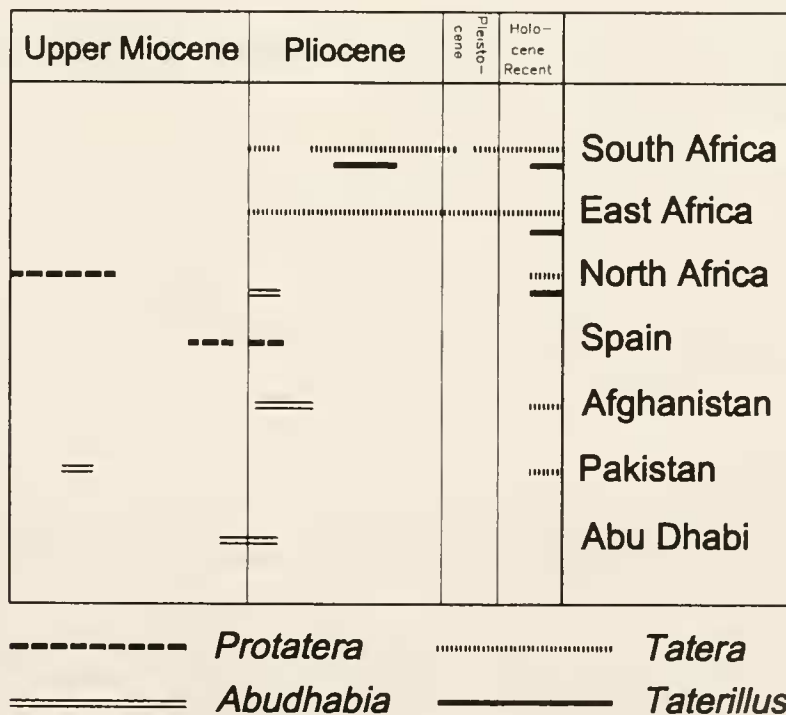


Figure 2: Distribution of Taterillinae: *Protatera*, *Tatera*, *Taterillus* and *Abudhabia*

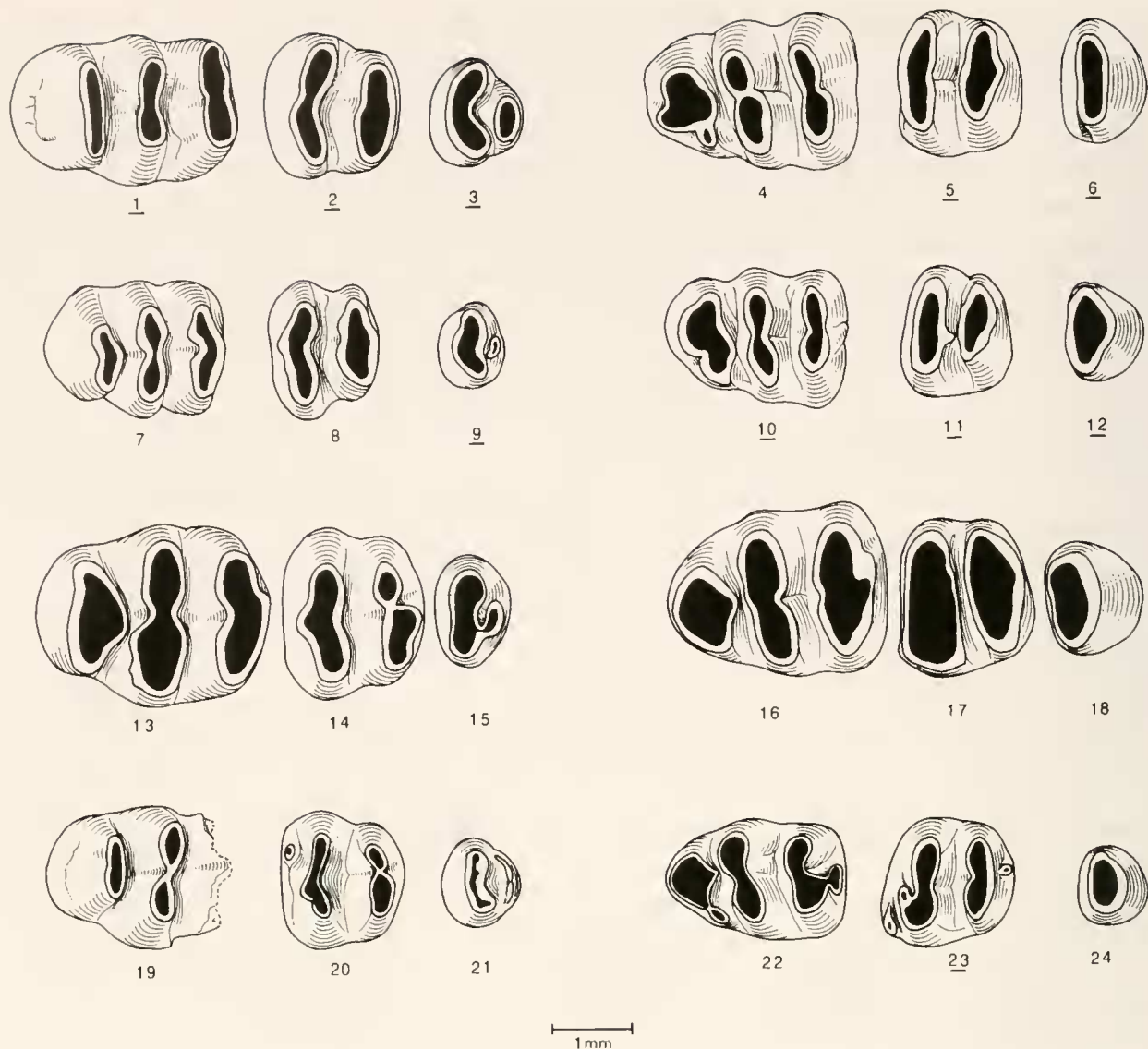


Plate 2: *Protatera algeriensis* from Amama 2 (Algeria): fig.1 M¹ dex (A2-1, holotype), fig. 2 M² dex (A2-2), fig.3 M³ dex (A2-3), fig.4 M₁ sin (A2-5), fig. 5 M₁ dex (a2-4), fig.6 M₃ dex (A2-7), JAEGER, 1977b.

Protatera almenarensis from Almenara (Spain): fig. 7 M¹ sin (ACS-M-11), fig.8 M² sin (ACS-M-42), fig. 9 M³ dex (ACS-M-02), fig.10 M₁ dex (ACS-M-33), fig.11 M₂ dex (ACS-M-03), fig.12 M₃ dex (ACS-M-37), AGUSTÍ, 1990.

Abudhabia kabulense from Pul-e Charki (Afghanistan): fig.13 M¹ sin (AFG211, holotype), fig.14 M² sin (AFG226), fig.15 M³ sin (AFG241), fig. 16 M₁ sin (AFG217), fig. 17 M₂ sin (AFG239), fig.18 M₃ sin (AFG246), SEN, 1983.

Abudhabia baynunensis from Abu Dhabi: fig. 19 M¹ sin (AAM572), fig. 20 M² sin (AAM574), fig.21 M³ sin (AAM575), fig. 22 M₁ sin (AAM566, holotype), fig. 23 M₁ dex (AAM567), fig. 24 M₃ sin (AAM570), DE BRUIJN & WHYBROW, 1994.

All specimens are figured as left cheek teeth; an underlined number denotes that the original is from the right side.

Protatera sp. from Pliocene deposits of Ibiza Island (Spain, MOYA-SOLA et al., 1984) is morphologically similar to *Protatera almenarensis* but larger, it must have settled on this island during the Messinian salinity crisis and got subsequently isolated (AGUSTÍ, 1990).

The Gerbillidae indet. from Gorafe 1&4, Caravaca and Botardo C are close to *Protatera*, but more material is needed for an allocation. The taxonomical position of *Protatera davidi* (GERAADS, 1998b) from the Lower Pliocene of Morocco remains uncertain, GERAADS concludes that a new genus seems probable, but more information on Miocene and Pliocene Gerbillidae

is needed (an allocation to the Gerbillinae is a possibility because of the presence of clearly grooved upper incisors in this species).

Abudhabia is known from the Upper Miocene of Pakistan (*Abudhabia* sp.; FLYNN & JACOBS, in press) it represents the oldest occurrence of this genus, it is more primitive in morphology than *Abudhabia kabulensis* (Plate 2, fig 13-18) from the Pliocene of Afghanistan (SEN, in press). *Abudhabia baynunensis* (Plate 2, fig 19-24), from the Upper Miocene from Abu Dhabia (DE BRUIJN & WHYBROW, 1994; DE BRUIJN, in press), seems to be the most primitive form. The geographical distribution of *Abudhabia* (Fig. 2), with the inclusion of the Libyan „*Protatera yardangi*“ is large (DE BRUIJN & WHYBROW, 1994).

Abudhabia can be seen as an ancestor for *Taterillus* (DE BRUIJN & WHYBROW, 1994). Fossil *Taterillus* specimens are reported from the Middle Pliocene of Botswana and Namibia (PICKFORD et al., 1992). Extant *Taterillus* occur only in Africa, they inhabit treeless plains, thorny scrub savannahs, and woodlands.

Subfamily Gerbillinae

The origin(s) of the Gerbillinae probably lies in myocricetodontines with a morphology as found in *Myocricetodon* group A species: with the reduction of the 'normal' longitudinal crest, without accessory cusps and with a simple anterocone. But it is not possible to indicate one specific group or species within the Myocricetodontinae as being ancestral to all Gerbillinae. AGUSTÍ (1991) indicates that the Gerbillinae are possible polyphyletic, the diverse genera of the Gerbillinae were probably derived from different Myocricetodontinae species.

The first Gerbillinae to occur, *Pseudomeriones* (Fig. 3), is reported from the Upper Miocene of Turkey and Afghanistan: *Pseudomeriones latidens* SEN 1998 (Plate 3, figs. 17, 18) (Sherullah and Molayan in Afghanistan; Karaözü and Kaleköy in Turkey). A slightly more evolved species, *Pseudomeriones abbreviatus* (Plate 3, figs 1-6) occurs slightly later in Dendil (Upper Miocene, Turkey). This species is also reported from the upper Miocene and Pliocene of China

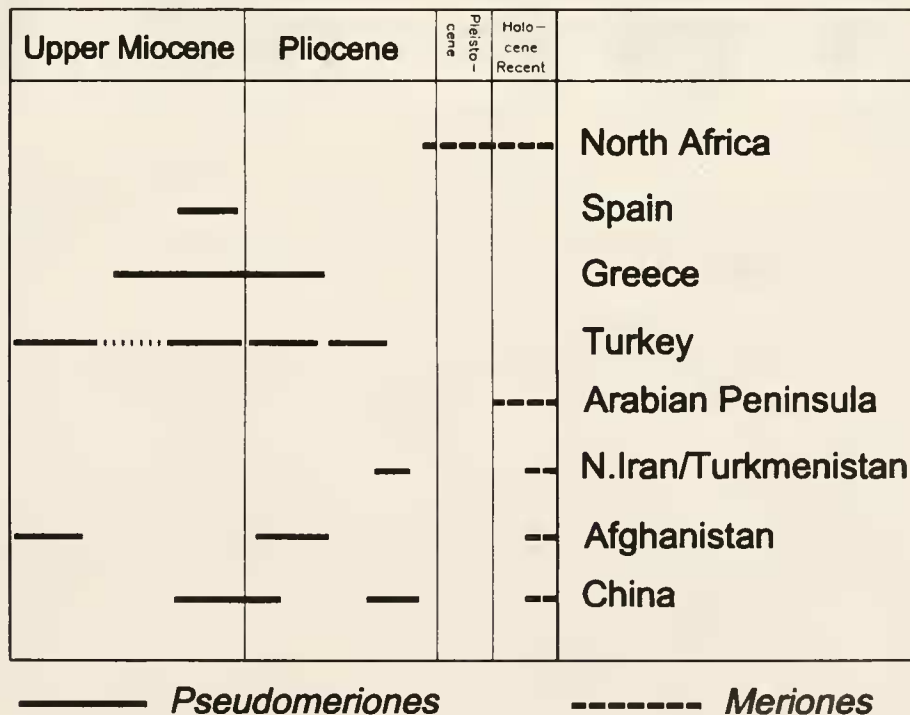


Figure 3: Distribution of Gerbillinae: *Pseudomeriones* and *Meriones*

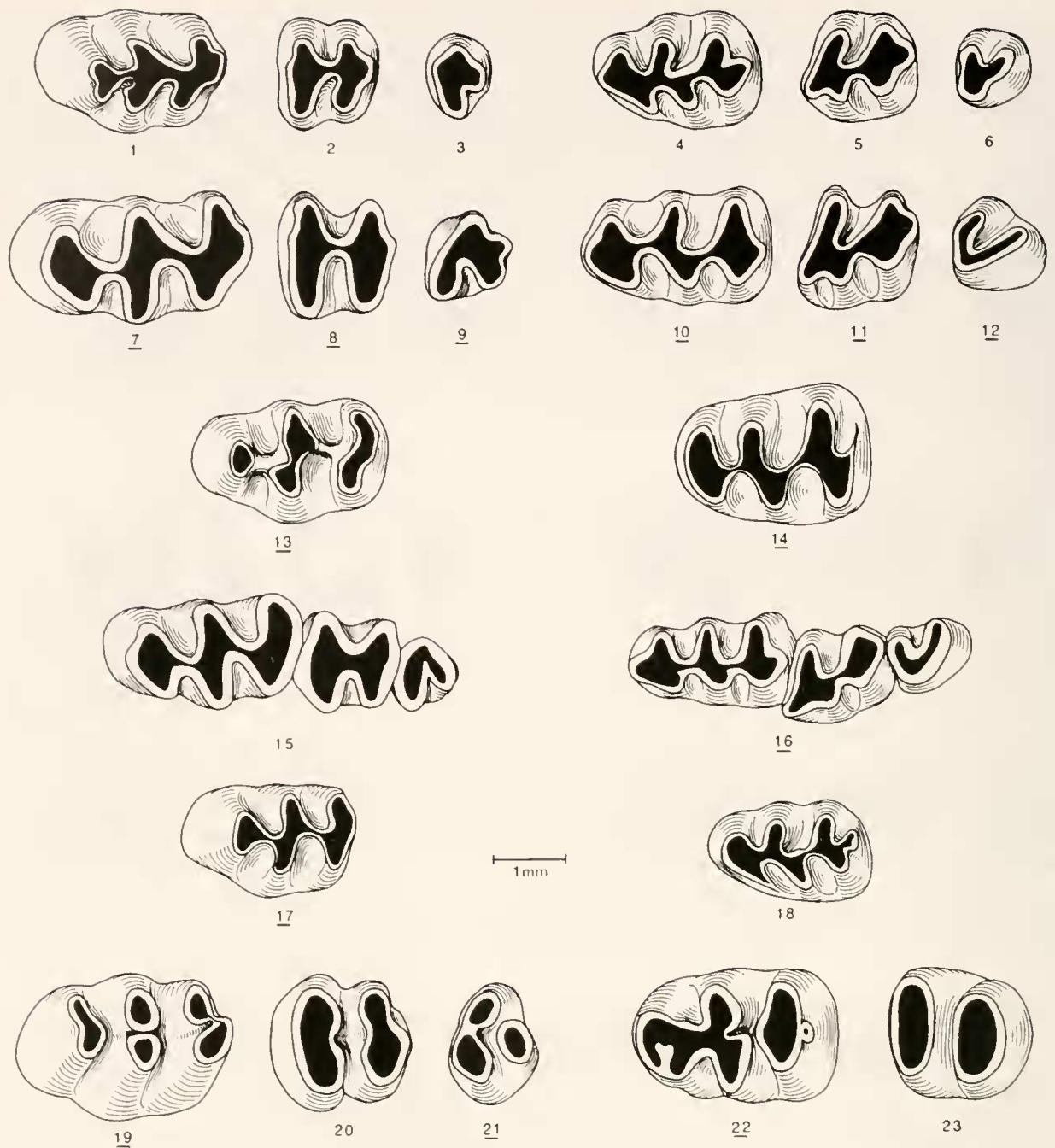


Plate 3: *Pseudomeriones abbreviatus* from Pul-e Charki (Afghanistan): fig. 1 M^1 sin (AFG253), fig. 2 M^2 sin (AFG286), fig. 3 M^3 sin (AFG343), fig. 4 M_1 sin (AFG370), fig. 5 M_2 sin (AFG370), fig. 6 M_3 sin (AFG383), SEN, 1983.

Pseudomeriones rhodius from Rhodos (Greece): fig. 7 M^1 dex (192), fig. 8 M^2 dex (171), fig. 9 M^3 dex (211), fig. 10 M_1 dex (164), fig. 11 M_2 dex (167), fig. 12 M_3 dex (187), DE BRUIJN et al., 1980.

Pseudomeriones pythagoresi from Samos (Greece): fig. 13 M^1 dex (CM36284), fig. 14 M_1 dex (CM36305, holotype), BLACK et al., 1980.

Pseudomeriones tschaltensis from Çalta (Turkey): fig. 15 M^{1-3} sin (ACA917), fig. 16 M_{1-3} dex (ACA974), SEN, 1977.

Pseudomeriones latidens from Molayan (Afghanistan): fig. 17 M^1 dex, fig. 18 M_1 sin, SEN, 1983.

Debruijnimys julii from Asta Regia (Spain): fig. 19 M^1 dex, fig. 20 M^2 sin, fig. 21 M^3 dex, fig. 22 M_1 dex (AR36, holotype), fig. 23 M_2 sin, CASTILLO & AGUSTÍ, 1996.

All specimens are figured as left cheek teeth; an underlined number denotes that the original is from the right side.

(Ertemte, Harr Obo), the Upper Miocene of Spain (Almenara-M) and the Lower Pliocene of Afghanistan (Pul-e Charki). Other *Pseudomeriones* species are *Pseudomeriones pythagorasi* (Plate 3, figs. 13-14) (Upper Miocene of Samos, Greece), *Pseudomeriones rhodius* (Plate 3, figs. 7-12) (Lower Pliocene of Maritsa, Rhodes, Ano Metochi and Monasteri, Greece), and *P. tchaltensis* (Plate 3, figs 15-16) (Upper Pliocene of Turkey). SEN (1983, 1998) and AGUSTÍ (1990) concluded that these species are very specialised and probably had a very limited geographical distribution.

All the *Pseudomeriones* species show a limited geographical and stratigraphical range of occurrence except *Pseudomeriones abbreviatus* which has the largest distribution. *P. latidens* seems to be the most primitive form of *Pseudomeriones* (SEN, in press). A possible evolutionary scenario for *Pseudomeriones* could be the transition of *P. latidens* into *P. abbreviatus* which migrated to China and Europe, where, in separated areas, it could develop into the more specialised forms.

Pseudomeriones is thought to be the ancestral form of *Mascaromys* (Uppermost Pliocene and lowest Pleistocene of North Africa) and *Meriones* (TONG, 1989). The oldest *Meriones* comes from the upper Pliocene of North Africa (Aïn Brimba, Tunisia) and the Pleistocene of North Africa (Maghreb). Extant *Meriones* occur mainly in Asia, the Arabian Peninsula and Northern Africa. *Meriones* species live in clay and sandy deserts, low plains, cultivated fields, grasslands and mountain valleys. They can adapt to a wide range of temperature and humidity.

Another member of the Gerbillinae, *Debruijnmys* (Fig.4 and Plate 3, figs 19-24), is recognised in Pliocene Spanish assemblages (Asta Regia, Bacochas 1, Alcoy, La Gloria 4). Before the gerbillines from Asta Regia (CASTILLO & AGUSTÍ, 1996) were found, the few gerbilline specimens from the Spanish Pliocene were seen as *Protatera* sp. or Gerbillidae indet. (AGUILAR et al., 1983; AGUSTÍ, 1991). The species from Asta Regia, *Debruijnmys julii*, has a longitudinal crest and are therefore not included in the Taterillinae. *Debruijnmys* sp. from Alcoy (Lower Pliocene) seems to be more primitive. CASTILLO & AGUSTÍ (1996) recognised this species also in the North African locality of Aïn Brimba (Upper Pliocene; Gerbillinae indet. TONG, 1989).

All other fossil Gerbillinae are found in Africa (Appendix II): *Gerbillus* in the Middle Pliocene of Botswana, the Upper Pliocene of North Africa (Marocco) and in the Pleistocene of North, East and South Africa. *Eulmus* occurs in the Middle Pliocene of North Africa and

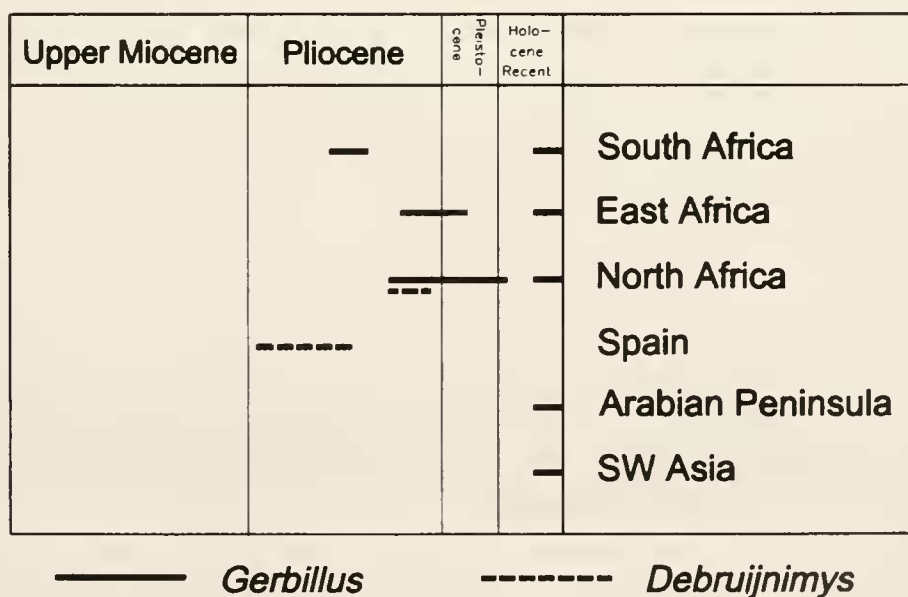


Figure 4: Distribution of Gerbillinae: *Gerbillus* and *Debruijnmys*

Psammomys occurs in the Late Pleistocene of Israel. In the Early Pleistocene of Asia *Rhombomys* is found. The status of 'Gerbillus' from Celleneuve (France) remains unclear.

Gerbillus, the most prominent extant member of the Gerbillinae, has at least 38 species and occurs in dry biotopes of Africa, the Arabian Peninsula and SW Asia (Fig.4). The origin of *Gerbillus* is not yet understood, fossil *Gerbillus* species are known from Upper Pliocene and Pleistocene deposits from North Africa and Israel respectively. Extant *Psammomys* is found in the Northern Part of Africa and the Arabian Peninsula and inhabits dry country with sometimes only scant vegetation. *Rhombomys* inhabits sandy and clay deserts in the foothills of the mountains of Central Asia.

Migrations of the European Gerbillidae

In North Africa two phases of migration in the upper Miocene are recognised (COIFFAIT, 1991). Rodents with European affinities are found in the localities of Aïn Gueterra (Morocco, BRANDY et al., 1980), La voie Fereé (Tunisia, ROBINSON et al., 1982), Argoub and Kemellal (Algeria, COIFFAIT, 1991) and Afoud (Marocco, BENAMMI, 1997).

The first phase is documented by the arrival of several European species: *Apodemus gudrunae*, *Stephanomys*, *Ruscinomys* and *Prolagus michauxi*. The oldest locality (Afoud 1) is thought to be 6.1 Ma (BENAMMI et al., 1995), so European elements occur in North Africa well before the Messinian. The second phase is documented in the locality of Aïn Gueterra with the presence of *Cricetus barreri*, *Apodemus jeanteti* and *Eliomys truci*. This took place about the Mio-Pliocene transition.

A migration just before the Messinian from North Africa into Spain (Salobreña and Almenara-M; AGUSTÍ, 1991) is documented by *Myocricetodon cf. parvus*, *Protatera almenarensis*, *Protolophiomys* and *Dendromus*. The faunal exchange could have taken place through the Betic-Rif area, which formed a corridor between South-western Europe and Africa at the end of the Miocene (BENAMMI et al., 1995).

Pseudomeriones and *Calomyscus* are also considered to be immigrants into Spain, they occur in Spanish Miocene localities (Salobreña, Almenara-M) and *Calomyscus* also in France (La Tour). These taxa are known from the eastern part of the Mediterranean and probably migrated to western Europe by the northern Mediterranean exchange (GERAADS, 1998a) to France and Spain.

The origin of *Debruijnimys* (Lower Pliocene of Spain, Alcoy) and Gerbillinae indet. in several other Spanish localities is unclear but a migration by the northern Mediterranean exchange seems probable (AGUSTÍ & LLENAS, 1996; GERAADS, 1998a).

In Greece *Pseudomeriones* and *Calomyscus* are both considered to be immigrants from eastern regions (Turkey, Afghanistan).

Acknowledgements

The plates and figures were made by W. Den Hartog, J. Luteyn and T. Van Hinte.

Drs. J. Agustí, D. Geraads, P. Mein and S. Sen are thanked for supplying valuable information. Dr. D.F. Mayhew corrected the English text. The support and the endless stream of information from Dr. Hans de Bruijn was indispensable.

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LOCALITIES IN SPAIN	MN zone / age	SPECIES	AUTHOR(S)	COLLECTION
Asta Regia	MN 15	<i>Debruijnimys julii</i>	CASTILLO & AGUSTÍ (1996)	UGS
Bacochas 1	MN 13/14	<i>Debruijnimys julii</i>	SESÉ (1989); CASTILLO & AGUSTÍ (1996)	NMS
La Gloria 4	MN 14	<i>Debruijnimys julii</i>	MEIN et al. (1990); CASTILLO & AGUSTÍ (1996)	NMS
Alcoy	MN 14	<i>Debruijnimys</i> sp.	CASTILLO & AGUSTÍ (1996)	CSS
Ibiza (Ses Fontanelles)	MN 14	<i>Protatera</i> sp.	MOYA-SOLA et al. (1984)	CSS
Gorafe 1&4	MN 14	Gerbillidae indet.	DE BRUIJN (1974); AGUSTÍ (1986)	UUN
Botardo C	MN 13/14	Gerbillidae indet.	AGUSTÍ (1989); AGUSTÍ (1991)	CSS
Caravaca	MN 13/14	Gerbillidae indet.	AGUSTÍ (1989); AGUSTÍ (1991)	CSS
Pino Mojón	MN 13	<i>Myocricetodon aff parvus</i>	SESÉ (1989)	NMS
Salobreña	MN 13	<i>Calomyscus cf. minor</i>	AGUILAR et al. (1984); AGUSTÍ (1991)	UMF
		<i>Protatera</i> sp.		
		<i>Myocricetodon aff. parvus</i>		
		<i>Calomyscus delicatus</i>		
Almenara-M (Casablanca-M)	MN 13	<i>Protatera almenarensis</i>	AGUILAR et al. (1984); AGUSTÍ (1991)	CSS
		<i>Myocricetodon</i> sp.		
		<i>Pseudomeriones abbreviatus</i>		
LOCALITIES IN FRANCE	MN zone / age	SPECIES	AUTHOR(S)	
Celleneuve	MN 14	"Gerbillus"	JAEGER & HARTENBERGER (1989)	UMF
La Tour	MN 13	<i>Myocricetodon</i> sp.	JAEGER & HARTENBERGER (1989)	UMF
		<i>Calomyscus</i> sp.		
LOCALITIES IN TURKEY	MN zone/ age	SPECIES	AUTHOR(S)	
Çalta	MN 15	<i>Pseudomeriones tchaltensis</i>	SEN (1977); SEN (1983)	MTA
Iödeli	MN 14	<i>Pseudomeriones</i> sp.	SÜMENGİN et al. (1990)	MTA
Suleimanlı	MN 13	<i>Calomyscus</i> sp.	DE BRUIJN pers. comm.	UUN
Dendil	MN 10	<i>Pseudomeriones cf. abbreviatus</i>	SÜMENGİN et al. (1990)	MTA
Karaözü	MN 10	<i>Pseudomeriones cf. latidens</i>	SÜMENGİN et al. (1990)	MTA
Kaleköy	MN 10	<i>Pseudomeriones cf. latidens</i>	SÜMENGİN et al. (1990)	MTA
Yeni Eskişehir	MN 7/8	<i>Myocricetodon eskishisarensis</i>	WESSELS et al. (1987)	MTA

LOCALITIES IN GREECE	Mn zone / age	SPECIES	AUTHOR(S)
Maritsa (Rhodos)	MN 14	<i>Pseudomeriones rhodius</i>	DE BRUIJN et al. (1970); SEN (1983)
<i>Calomyscus minor</i>			
Kalithies	MN 14	<i>Pseudomeriones</i> sp.	DE BRUIJN (1989); BLACK et al. (1980)
Ptolomais (Lower FM, sect. 6)	MN 13/14	<i>Pseudomeriones</i> sp.	DE BRUIJN per. comm.
Monasteri	MN 13	<i>Pseudomeriones rhodius</i>	DE BRUIJN (1989)
Ano Metochi 3	MN 13	<i>Pseudomeriones</i> sp.	DE BRUIJN (1989)
Samos S3	MN 12	<i>Pseudomeriones pythagorasi</i>	BLACK et al. (1980)
UUN - Faculty of Earth Sciences, University of Utrecht, the Netherlands			
MTA - Maden Tetkik ve Arama Enstitüsü, Ankara, Turkey			
CMU - Carnegie Museum of Natural History, USA			
CSS - Institut de Paleontologia AM. Crusafont, Sabadell, Spain			
UGS - Department of Stratigraphy and Paleontology of the University of Granada, Spain			
UMF - Université des Sciences et Techniques du Languedoc, Montpellier, France			
NMS - Museo Nacional de Ciencias Naturales, Madrid, Spain			

Appendix II: Fossil occurrences of Gerbillidae in Europe, Africa and Asia

<i>Mystromys</i>					
Pliocene-Pleistocene	South Africa		LAVOCAT (1978); POCOCK (1987); SENUT et al. (1992); DENYS (1991); AVERY (1995)		
<i>Calomyscus</i>					
Upper Miocene-Lower Pliocene	SE Europe		DE BRUIJN et al. (1970); SEN (1983)		
Upper Miocene	SW Europe		AGUILAR et al. (1984); JAEGER & HARTENBERGER (1989); AGUSTI (1991)		
<i>Myocricetodon</i>					
Upper Miocene	Arabian Peninsula		DE BRUIJN & WHYBROW (1994)		
Upper Miocene	SW Europe		AGUILAR et al. (1984); AGUSTI (1991); SESÉ (1989); JAEGER & HARTENBERGER (1989)		
Middle Miocene - Lower Pliocene	North Africa		JAEGER (1977a,b); BERNOR (1982); HEISSIG (1982); TONG (1989); COIFFAIT (1991); BENAMMI et al. (1995); GERAADS (1998b)		
Middle Miocene	South Africa		SENUT et al. (1992)		
Middle Miocene	East Africa		TONG & JAEGER (1993)		
Miocene	Pakistan		WESSELS et al. (1987); LINDSAY (1988); WESSELS (1996)		
<i>Zramys</i>					
Middle-Upper Miocene	North Africa		JAEGER et al. (1973); JAEGER (1977a,b) AMEUR (1979); ROBINSON et al. (1982); COIFFAIT (1991); BENAMMI et al. (1995)		
<i>Dakkamys</i>					
Middle Miocene	North Africa		JAEGER (1977a); COIFFAIT (1991)		
Middle-Upper Miocene	Pakistan		LINDSAY (1988); WESSELS (1996)		
<i>Mellalomys</i>					
Middle Miocene	North Africa		JAEGER (1977a); COIFFAIT (1991); BENAMMI et al. (1995); BENAMMI (1997)		
Lower-Middle Miocene	Pakistan		LINDSAY (1988); WESSELS (1996)		
<i>Shamalina</i>					
Lower Miocene	Arabian Peninsula		WHYBROW et al. (1982)		

- Punjabemys*
Lower-Middle Miocene
Pakistan
LINDSAY (1988); WESSELS (1996)
- Aissamys*
Middle Miocene
North Africa
COIFFAIT (1991)
- Sindemys*
Lower and Middle Miocene
Pakistan
WESSELS (1996)
- Tatera*
Pliocene-Pleistocene
East Africa
LAVOCAT (1965); SABATIER (1982); DENYS (1983); WESSELMAN (1984);
BLACK & KRISHTALKA (1986)
- Lower Pliocene-Pleistocene
South Africa
LAVOCAT (1978); HENDEY (1984); PICKFORD & MEIN (1988);
PICKFORD et al. (1992); SENUT et al. (1992); Avery (1995)
- Taterillus*
Upper Pliocene
South Africa
POCOCK (1987); PICKFORD & MEIN (1988)
- Gerbillurus*
Upper Pliocene-Pleistocene
South Africa
LAVOCAT (1978); SENUT et al. (1992)
- Protatera*
Upper Miocene/ Lower Pliocene
Upper Miocene
SW Europe
North Africa
AGUILAR et al. (1984); MOYA-SOLA et al. (1984); AGUSTI (1990)
JAEGER (1977b); COIFFAIT (1991)
- Abudhabia*
Lower Pliocene
Lower Pliocene
Upper Miocene
Upper Miocene
Afghanistan
North Africa
Arabian Peninsula
Pakistan
SEN (1977)
MUNTHE (1987)
DE BRUIJN & WHYBROW (1994); DE BRUIJN (in press)
FLYNN & JACOBS (in press)

<i>Gerbillus</i>	Upper Pliocene-Pleistocene Upper Pliocene-Pleistocene Middle Pliocene	North Africa East Africa South Africa	TONG (1989); GERAADS (1993) LAVOCAT (1965); WESSELMAN (1984); TONG (1989) LAVOCAT (1978); PICKFORD & MEIN (1988)
<i>Meriones</i>	Pleistocene Upper Pliocene	North Africa Israel	TONG (1989); MEIN & BESANCON (1993) HAAS (1966); TCHERNOV & CHETBOUN (1984)
<i>Pseudomeriones</i>	Pliocene Upper Miocene-Pliocene Upper Miocene-Pliocene	Turkmenistan SE Europe China	BIRMAN et al. (1971) SEN (1977, 1983); BRUNET et al. (1980); BLACK et al., 1980; DE BRUIJN 1989; SUMENGEN et al. (1990)
	Upper Miocene Upper Miocene	Afghanistan SW Europe	TEILHARD DU JARDIN (1926); YOUNG (1927); SCHAUB (1934); FAHLBUSCH et al. (1983); Qiu (1988); LI et al. (1984) SEN (1983; in press) AGUILAR et al. (1984); AGUSTÍ (1990, 1991)
<i>Desmodillus</i>	Upper Pliocene-Pleistocene	South Africa	AVERY (1995); SENUT et al. (1992)
<i>Mascomys</i>	Upper Pliocene	North Africa	TONG (1986, 1989)
<i>Eulmus</i>	Upper Miocene-Pliocene	North Africa	AMEUR (1991)
<i>Debruijnimys</i>	Pliocene Pliocene	Spain North Africa	SESÉ (1989); CASTILLO & AGUSTÍ (1996); MEIN et al. (1993) CASTILLO & AGUSTÍ (1996)